DISJUNCTIVE DISTRIBUTIONS IN THE
LICHEN-FORMING FUNGI[1]

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There is a widespread notion among botanists that the nonvascular cryptogams are easily disseminated, ubiquitous plants without well defined geographic ranges. Certainly for many groups, such as the fresh-water algae and the nonpathogenic or nonsubstrate-specific microfungi, this view seems to be justified, for few meaningful geographic-to-taxonomic correlations among these organisms have been perceived. In other groups, for example the higher Basidiomycetes, our ignorance of phytogeographically significant ranges may reflect only the magnitude of the problems inherent in the study of organisms known only from ephemeral sporocarps. There are, however, two large groups of cryptogams in which species and taxa of higher than specific rank show well marked geographic distributions, including disjunctive ones, like those known in the vascular plants. These are the bryophytes and the lichens, the only major groups of terrestrial nonvascular cryptogams in which the vegetative plant body is exposed and perennating. The aim of this paper is to examine disjunction as it is known with regard to the second group, the lichen-forming fungi.

Reliable distribution maps have been published for few (only hundreds) of the approximately 20,000 recognized species of lichen fungi. Most of the best substantiated distributions are for conspicuous foliose or fruticose species from temperate regions of the northern hemisphere. To underline the point that lichen fungi may have geographic ranges comparable to those of vascular plants, Table 1 gives eight pairs of common, locally abundant, native North American plants, in each case a lichen fungus and a tree, for which the total geographic ranges are almost congruent or very highly comparable. It should be pointed out that although all but one of the lichen examples are epiphytes, none is ecologically restricted to the bark of the tree species to which its range is compared. Many more such examples could be given from the flora of North America and the floras of Europe and the Far East. So similar in fact are the well documented ranges of lichens to the ranges of vascular plants that the conclusion that both result from the same physioecological and historical factors is inescapable.

TYPES OF DISJUNCTIVE DISTRIBUTIONS IN LICHEN FUNGI

Most plant species can be said to have disjunctive ranges if the concept of what continuity of distribution consists of is sufficiently narrowed. The types of disjunctions that I shall discuss, however, are major ones in which centers of modern ranges are on different continents. Disjunction could as well be discussed in a more restricted framework for the examples of North American and European

TABLE 1. Eight pairs of common, native North American species, a lichen and a tree, in which the total geographic ranges are nearly congruent or highly similar. [Ranges of trees from Little (1971); ranges of lichens from various authors.]

Lichen Species	Tree Species
Actinogyra muehlenbergii (Ach.) Schol.	Tsuga canadensis (L.) Carr.
Anzia colpodes (Ach.) Stizenb.	Quercus palustris Muenchh.
Dermatocarpon tuckermanii (Rav.) Zahlbr.	Carya ovata (Mill.) K. Koch
Parmelia caroliniana Nyl.	Diospyros virginiana L.
Parmelia livida Tayl.	Cornus florida L.
Physcia millegrana Degel.	Juniperus virginiana L.
Platismatia herrei (Imsh.) Culb. & Culb.	Picea sitchensis (Bong.) Carr.
Pseudevernia cladonia (Tuck.) Hale & Culb.	Picea rubens Sarg.

lichen species disjunctive in their own native continent are numerous. I have selected my examples of disjunctive ranges from those species with distributions including the New World in the hope that comparisons to species of other plant groups discussed in this symposium may become apparent. I have attempted to minimize the inaccuracies that accompany insensitive taxonomies by restricting my examples to taxa 1) that are well-known systematically (even if their taxonomic rank is in dispute), 2) that have been recently studied, 3) that are common in at least part of their range, and 4) that are large enough to be conspicuous (and consequently often collected). Some of my examples may not satisfy all these criteria, but most of them do.

1. Widespread disjunctions.—Many taxonomically well-defined species have extremely broad ranges and are represented on most continents. This is often pointed to as evidence that evolution in the lichens is (or has become) very slow. The following species occur on at least four continents:

Cladonia merochlorophaea Asah.　　　　　Peltigera polydactyla (Neck.) Hoffm.
Heterodermia leucomelaena (L.) Poelt　　Sphaerophorus melanocarpus (Sw.)
Menegazzia terebrata (Hoffm.) Mass.　　　　　　　　　　　　　　　　DC.
Normandina pulchella (Borr.) Nyl.　　　　Thamnolia vermicularis (Sw.)
Parmelia crinita Ach.　　　　　　　　　　　　　　　　　Ach. ex Schaer.

There are also large numbers of pantropical species, for example:

Baeomyces absolutus Tuck.　　　　　　　　Heterodermia tremulans (Müll. Arg.)
Cladonia aggregata (Sw.) Ach.　　　　　　　　　　　　　　　　　Culb.
Cladonia balfourii Del.　　　　　　　　　　Graphis afzelii Ach.
Dirinaria aegialita (Ach.) B. Moore　　　　Parmelia cristifera Tayl.
　　　　　　　　　　　　　　　　　　　　Parmelia tinctorum Del. ex Nyl.

The two lists above include some species that reproduce by sexual means through ascospores that must find an appropriate algal partner and others that reproduce primarily by asexual propagules—soredia or isidia, structures that are composed of both hyphal fragments and algal cells and constitute a prolific source of "instant" lichens. But among the widely distributed species, the production of asexual propagules is doubtless more common than among the lichens

as a whole. The recently monographed *Parmelia* subgen. *Amphigymnia* (Hale, 1965) provides data that may well prove to be typical for many widely distributed genera of lichen fungi: There are 26 pantropical species of *Parmelia* subgen. *Amphigymnia* of which only 5 (19%) lack soredia or isidia. Although circumstantial evidence confirms the great importance of soredia and isidia as effective propagules, direct observation of the dissemination of these bodies is infrequent. It has been shown experimentally that soredia are indeed detached and carried by wind (Bailey, 1966). Soredia have also been recovered from samples of air-borne plant fragments (Rudolph, 1970), but most soredia in samplings from the air are probably recorded as algae and not recognized for what they are.

In the category of widespread disjunctions one might include very large numbers of lichen species with enigmatic disjunctive ranges—for example *Parmelia latissima* Fée, which occurs in tropical America and India. Are such distributions the result of long-distance dispersal or are they the relics of earlier and broader ranges? Definitive explanations of such ranges are simply not possible in groups such as the lichen fungi that lack a fossil record.

2. *Circumboreal disjunctions.*—The following arctic and north-temperate species have circumboreal, disjunctive ranges:

Alectoria nidulifera Norrl.
Cetraria halei Culb. & Culb.
Cetrelia cetrarioides (Del. *ex* Duby)
            Culb. & Culb.
Evernia mesomorpha Nyl.
Lobaria linita (Ach.) Rabenh.

Nephroma arcticum (L.) Torss.
Parmeliopsis ambigua (Wulf.) Nyl.
Peltigera horizontalis (Huds.) Baumg.
Solorina saccata (L.) Ach.
Umbilicaria arctica (Ach.) Nyl.
Xanthoria fallax (Hepp) Arn.

The disjunctions of some circumboreal species are maintained by narrow amplitudes of ecologic tolerance. For example, the extremely oceanic species *Platismatia norvegica* (Lynge) Culb. & Culb. occurs in the oceanic parts of Scandinavia (main European range), in Scotland, in Newfoundland, and along the North American West Coast from Oregon to southern Alaska (main American range). However, no obvious ecological factors limit the distribution of the tundra lichen *Asahinea chrysantha* (Tuck.) Culb. & Culb., which occurs continuously over large parts of Siberia and Alaska (main range) and locally on Baffin Island and in northern Scandinavia. The main range of this species would seem to have developed from gradual spread from a center of origin with the outliers the result of long-distance dispersal. Unlike *Platismatia norvegica, Asahinea chrysantha* does not seem to be limited to a specialized environment by a restrictive physiology.

3. *Bipolar disjunctions.*—Although some of the examples of lichens with bipolar disjunctive distributions pointed out by Du Rietz 30 years ago are perhaps to be challenged upon faulty taxonomy, the fact that this distribution type exists among the lichens is irrefutable. The best documented example is in the recently monographed genus *Platismatia* (Culberson & Culberson, 1968). The temperate species *P. glauca* (L.) Culb. & Culb. is locally very abundant in northern and western Europe, in northern North America, and in extreme southern Argentina

and Chile. The species is apparently absent from the high mountains of western South America. Long-distance dispersal of this sorediate species would seem to have been the origin of the antipodal population. This explanation is supported by the occurrence of *P. glauca* on Mt. Aberdare, Kenya, and Mt. Kilimanjaro, Tanzania, localities in east-central Africa about 5,000 km south of the southern limit of the European range of the species. Curiously, this widespread species does not occur in Himalaya, Japan, or Southeast Asia but is replaced there by a very distinctive vicariad, *P. erosa* Culb. & Culb.

4. *Europe-North America disjunctions.*—Some species occur in Europe and North America but are unknown elsewhere. Good examples are *Parmelia quercina* (Willd.) Vain. (widespread in southwestern Europe, locally common in California), *P. hypoleucina* J. Stein. (occasional in the Mediterranean Basin, common in the North American Atlantic Coastal Plain, rare in southern California), and *Letharia vulpina* (L.) Hue (locally common in the mountains of Central Europe, Morocco, and western North America). It is never possible to exclude long-distance dispersal as the explanation, but it is tempting to see these present ranges as the relicts of more extensive distributions before the separation of the continents.

5. *Eastern North America-Japan disjunctions.*—The early appreciated and now classic affinities between the floras of eastern Asia and eastern North America are well represented among the lichen fungi. In the vascular plants the floristic affinities are usually revealed through vicarism, but in the lichens some species are common to both regions. The following are all lichens known to me to be restricted to the regions in question and to be so uniform that both the eastern Asiatic and the eastern North American representatives are considered to be conspecific:

Anaptychia palmulata (Michx.) Vain.	*Lobaria quercizans* (Michx.) Vain.
Anzia ornata (Zahlbr.) Asah.	*Parmelia aurulenta* Tuck.
Candelaria fibrosa (Fr.) Müll. Arg.	*Parmelia formosana* Zahlbr.
Cladonia submitis Evans	*Parmelia galbina* Ach.
Cladonia clavulifera Vain.	*Pyxine sorediata* (Ach.) Mont.
Lobaria erosa (Eschw.) Nyl.	*Stereocaulon tennesseense* Magn.

It will be noted that all twelve of the above species are either foliose or fruticose. Surely as the crustose lichens become better known, the number of examples of this distribution type will be multiplied.

A relatively large number of other species have their main distributions in Japan and eastern North America but are also known elsewhere. *Actinogyra muehlenbergii* (Ach.) Schol. and *Heterodermia hypoleuca* (Ach.) Trev. are examples, the former occurring additionally in Siberia and the latter occurring additionally in Himalaya. *Umbilicaria caroliniana* Tuck. occurs on the highest peaks of the Southern Appalachians and in the mountains of Honshu and is known additionally from unglaciated parts of Alaska and from one locality in Siberia. *Cetrelia chicitae* (Culb.) Culb. & Culb. is one of the commonest lichens in the mountains of the eastern United States and of central Japan. It is also known
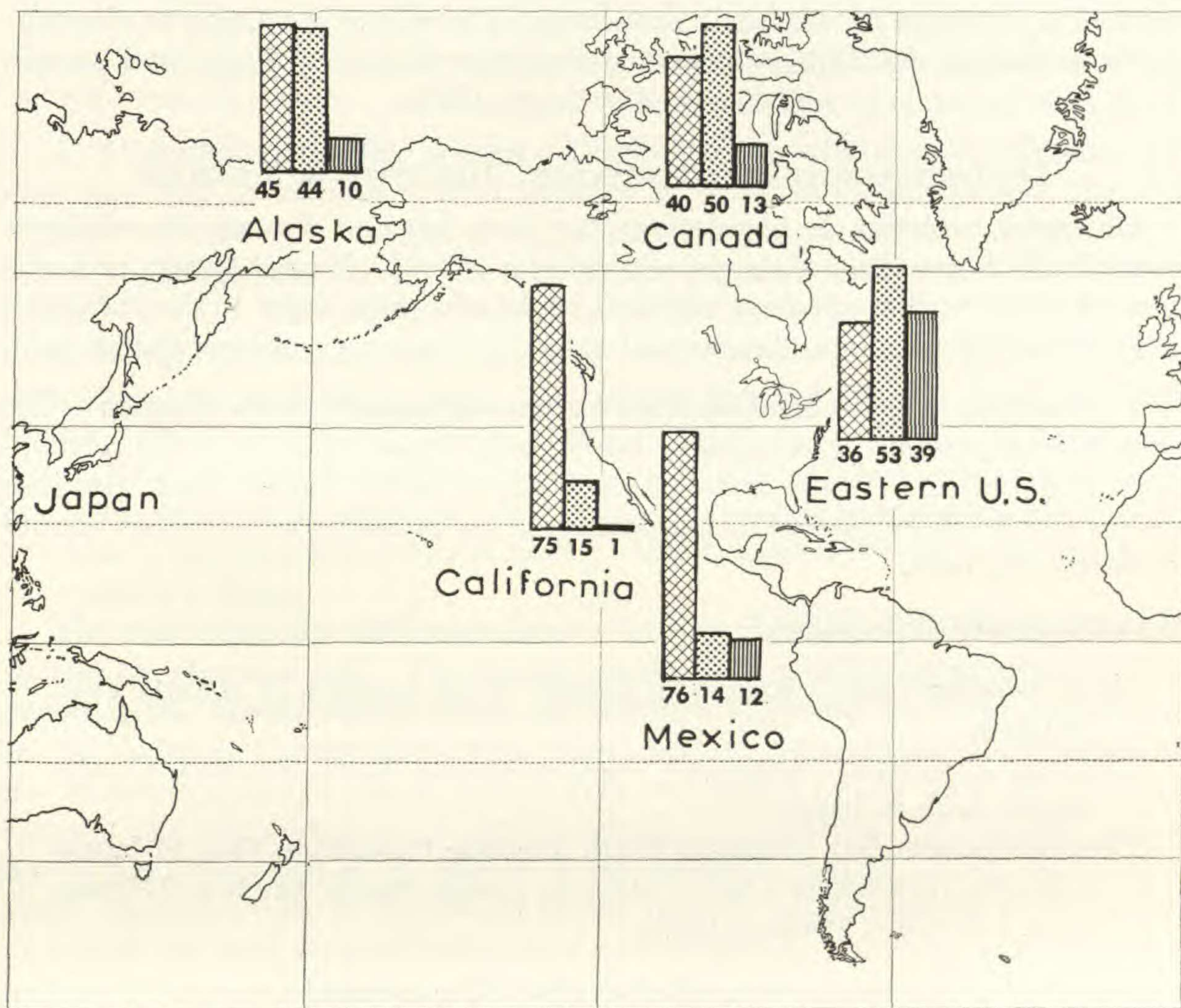
FIGURE 1. Comparison of the *Cladonia* flora of Japan (90 species) with that in various parts of North America. From left to right the columns refer to the number of species present in Japan but absent from the indicated region (cross hatched), the number of species common to Japan and the indicated region (stipple), and the number of species absent from Japan but present in the indicated region (vertical lines). Redrawn from Yoshimura (1968).

from a single locality in Europe (in the Vosges) and from a few mountain stations in Southeast Asia.

The large and diverse genus *Cladonia* is well represented in Japan and North America and is better known there than elsewhere for having attracted the attention of perceptive chemotaxonomists in both countries. Summarizing our present knowledge of the genus, Yoshimura (1968) showed that the number of species common to floras in various parts of North America and to the flora of Japan varies greatly. The number of species shared is greater in Alaska, Canada, and the East and smaller in California and Mexico, underlining the classic relationship among the species of an entire genus (Fig. 1).

The explanation of the origin of the eastern Asiatic-eastern North American vicarism is surely the same as that for the vicarism seen in the vascular plants of these regions—namely, that a richly diverse and once continuous Tertiary vegetation that extended from North America through the then adjoining continent of Europe and across Asia to Japan was subsequently reduced to widely separated

relictual populations by wholesale extinctions. The role of glaciation in eliminating from Europe the Tertiary lichen species now shared by Japan and eastern North America has been well discussed by Poelt (1963).

Disjunction with Differentiation: The Origin of Vicariads

Divergent evolution in populations that have become disjunct for whatever reason leads to speciation if the process goes far enough. It must always be borne in mind however, that apparent vicariads might owe their origin to the extinction in the disjunct populations of reciprocal members of a once sympatric species pair.

1. Vicariads in Japan (and/or eastern Asia) and eastern North America.—The most striking example of vicarism in lichen fungi comes again from the relationships of the eastern Asiatic and eastern North American floras. Such vicarious species may be differentiated by morphology or by chemistry of secondary natural products or by both.

Morphologically differentiated:

> *Anzia colpodes* (Ach.) Stizenb. in eastern North America; *A. colpota* Vain. in Japan.
> *Cladonia caroliniana* (Schwein.) Tuck. in eastern North America; *C. nipponica* Asah. in Japan.
> *Parmelia rudecta* Ach. in eastern North America; *P. ruderata* Vain. in Japan.
> *Umbilicaria mammulata* (Ach.) Llano in eastern North America; *U. esculenta* (Miyoshi) Minks in Japan.

Chemically (and in some also morphologically) differentiated:

> *Cladonia evansii* Abb. (atranorin and accessory usnic acid) in eastern North America; *C. pseudevansii* Asah. (usnic acid) in Japan.
> *Cladonia atlantica* Evans (baeomycesic and squamatic acids) in eastern North America; *C. hondoensis* Asah. (barbatic acid) in Japan.
> *Cladonia cristatella* Tuck. (barbatic and didymic acids) in eastern North America; *C. pseudomacilenta* Asah. (squamatic acid) in Japan.
> *Cladonia uncialis* (L.) Wigg. (accessory squamatic acid) in eastern North America; *C. pseudostellata* Asah. (hypothamnolic acid) in Japan and Alaska.
> *Cladonia cylindrica* (Evans) Evans (grayanic acid) in eastern North America; *C. norikurensis* Asah. (merochlorophaeic acid) in Japan.
> *Cladonia didyma* (Fée) Vain. (barbatic acid) in eastern North America; *C. pseudodidyma* Asah. (accessory bellidiflorin) in Japan.

The title of this section implies that the divergence that produced the ten species pairs listed above took place after rather than before isolation by disjunction. It could be argued, however, that all these species were present throughout the extent of the Tertiary forest and that in each pair, *A* and *B*, *A* became extinct in Asia and *B* became extinct in North America. This explanation cannot be categorically ruled out for some of the vicariad pairs. But it makes an unconvincing explanation for the whole list, because one would not expect every pair of

micro- or sibling species to have followed such a pattern of reciprocal extinctions. There should be at least a few pairs of microspecies still present in both places but not found elsewhere—yet I know not a single example.

2. *Ubiquitous collective species.*—Disjunctions in wide-spread collective species may lead to sufficient differentiation of the isolated populations that the regional elements are recognized taxonomically. Morphological (as opposed to chemical) differentiation can be seen in the common reindeer lichen, *Cladonia rangiferina* (L.) Web. subsp. *rangiferina* (circumboreal), and its regional derivatives subsp. *grisea* Ahti (eastern Asia), var. *abbayesii* Ahti (Mexico, Central America), and var. *vicaria* (Sant.) Ahti (Patagonia, Antarctica). Three common, closely related umbilicate lichens appear to owe their differentiation to past disjunction: *Lasallia pustulata* (L.) Mér. is common in Europe and rare in northern North America, *L. papulosa* (Ach.) Llano is common in subboreal and higher-elevation temperate eastern North America, and *L. asiae-orientalis* Asah. represents the complex in Japan.

The most enigmatic differentiations to be seen in widely distributed collective species are chemical ones. The already mentioned *Parmelia hypoleucina* J. Stein. occurs in the Mediterranean Basin and southern California and very abundantly on the Atlantic Coastal Plain from Cape Cod to Mississippi. But throughout the east-central section, from central Texas to southern New York and northern Georgia, the morphologically indistinguishable *P. hypotropa* Nyl. abounds and is one of the commonest of all eastern North American lichens outside the Coastal Plain. Phenotypically *P. hypotropa* differs from *P. hypoleucina* in being unable to convert its most abundant secondary natural product, norstictic acid, to stictic acid as *P. hypoleucina* does. Although this chemical change is a minor one—a one-step methylation that could conceivably be mediated by a single enzyme controlled by a single gene—the demonstrable but small chemical difference in the two populations must be linked to factors governing prodigious differences in physiological potential. *Parmelia hypotropa*, the dominant North American representation of the complex, seems to have been derived from the much older and (on a world-wide scale) still more widely distributed one.

An even more enigmatic case of chemical differentiation perhaps related to disjunction can be seen in the genus *Thamnolia*, which is monotypic or ditypic depending upon the weight assigned to chemistry. In spite of being totally asexual, *Thamnolia* is one of the most successful of all lichen genera, occurring abundantly on bare soil and among herbs throughout the arctic and alpine regions of the world. Individuals belong to one or the other of two chemical types: they produce either a pair of β-orcinol-type *para*-depsides (baeomycesic and squamatic acids) or a β-orcinol-type *meta*-depside (thamnolic acid). The constituent(s) of a given specimen can be determined only by appropriate chemical analysis, and consequently the abundant representation of the genus in herbaria constitutes a world-wide random sample of the chemical variation. By testing herbarium specimens Sato (1968) demonstrated that the *para*-depsides are produced exclusively or more commonly in populations in the northern hemisphere while the *meta*-depside is produced exclusively or more commonly in populations in the southern hemisphere, even though most populations in both
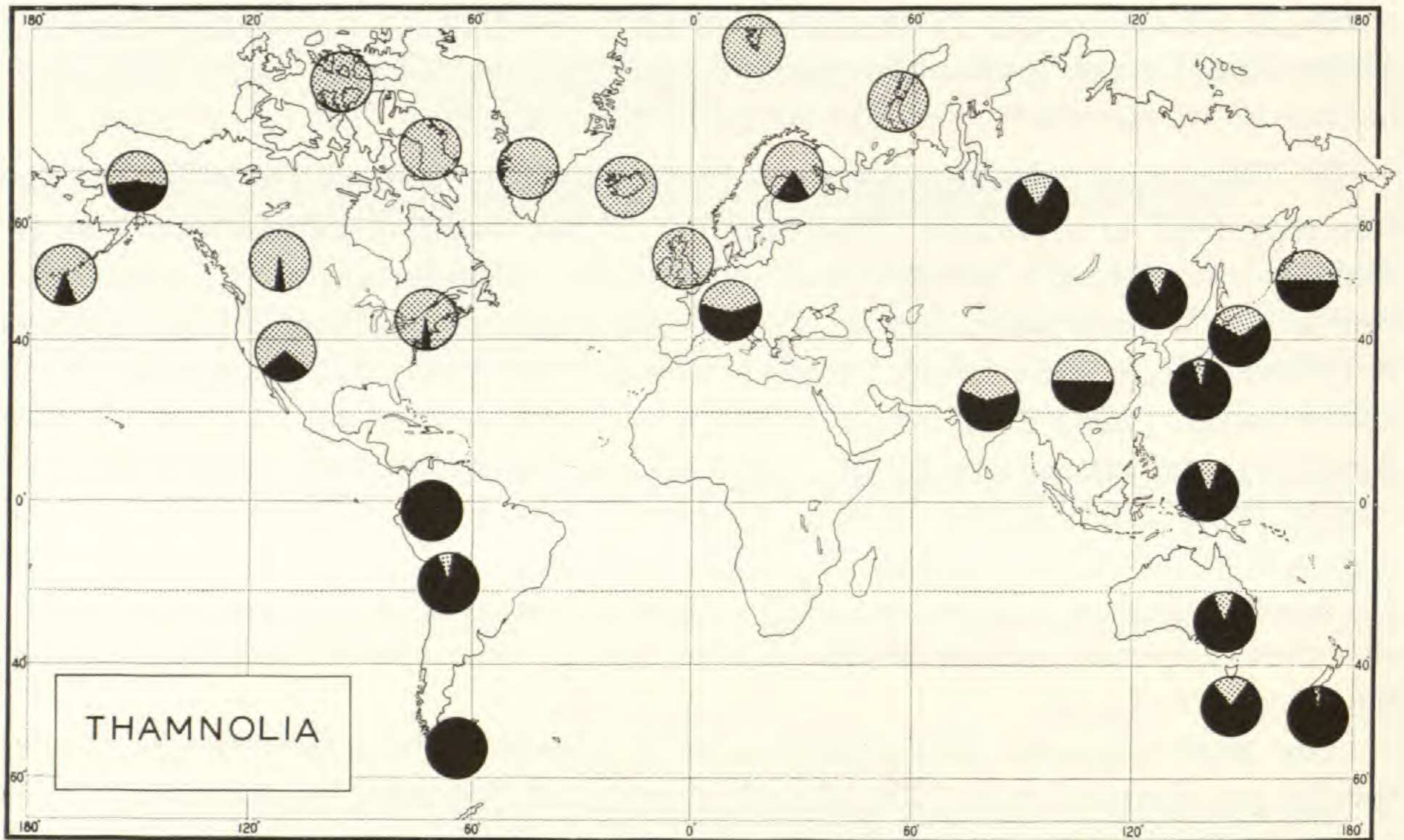
FIGURE 2. The proportion of the *Thamnolia* vegetation in various parts of the world consisting of *para*-depside producers (stipple) [= *T. subuliformis* (Ehrh.) Culb.] and *meta*-depside producers (black) [= *T. vermicularis* (Sw.) Ach. *ex* Schaer.]. Redrawn from Sato (1968).

hemispheres contain both chemical types (Fig. 2). Are these differences to be interpreted as coming from an allopatric differentiation in populations that have subsequently become extensively sympatric? The chemical differences involved are sufficiently complex that they would seem to reflect more than a superficial genetic modification and to require more than a simplistic explanation.

DISJUNCTION AND CONTINENTAL DRIFT

Although certain Old World-New World lichen distributions may owe their origin to the ancient connection of these land masses, long-distance dispersal usually seems a more reasonable explanation. One body of information, however, can be interpreted only in relation to the now known geological events that produced the Atlantic Ocean.

Parmelia subgen. *Amphigymnia* is a natural, well defined taxon of 106 species. Its botany and chemistry are well known thanks to Hale's (1965) recent monograph, and the plants are so large and conspicuous that they are well represented in herbaria. Figure 3 shows the number of species that occur in various parts of the world and the number of species endemic there. It will be noted that most of the species occur in Africa (64 species: 60% of the total), South America (51; 48%), Central America and Mexico (47; 44%), and North America (25; 24%). Thirty (28%) of the species are endemic to the New World, 22 (21%) are endemic to Africa, and 7 species are found only in tropical America and Africa. Fewer species occur in Europe (8; 8%) and Australia-New Zealand (17; 16%), and none of these are endemic. Most of the southern Asiatic and Pacific representation is drawn from the group of 26 pantropical species. Significantly 21 (81%) of the pantropical
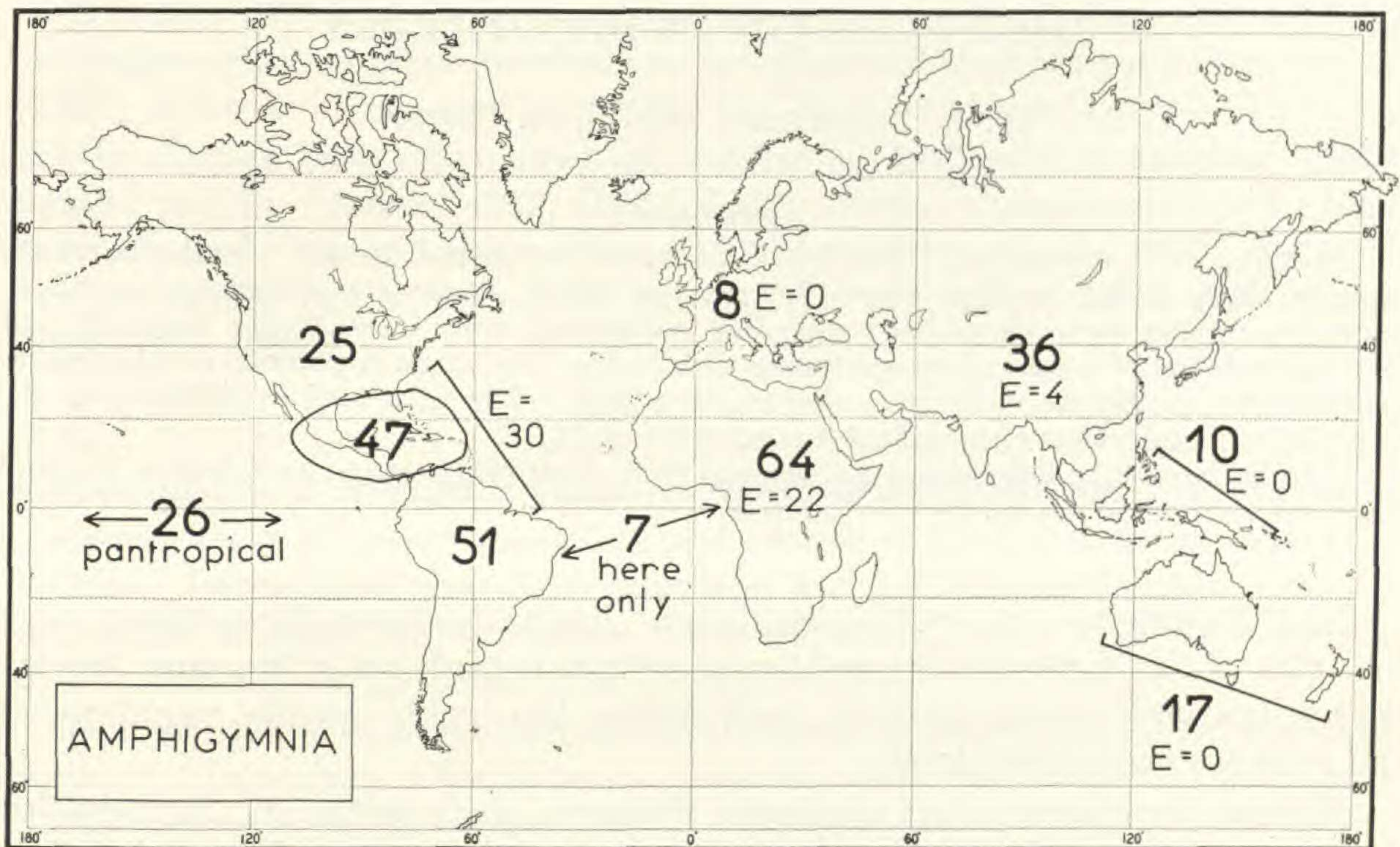
FIGURE 3. The numbers of species of *Parmelia* subgen. *Amphigymnia* in various parts of the world (larger-size numbers) and the number of endemic (*E*) species in each region (smaller-size numbers). Seven species are found only in Africa and South America. Data taken from Hale (1965).

species produce asexual propagules. *Parmelia* subgen. *Amphigymnia* must have been well differentiated before the New World separated from the Old some 100 million (?) years ago and its present disjunctive distribution is due primarily to historical events and secondarily to long-distance dispersal.

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